神经兴奋性、峰值和簇发放的分岔机制
Section 7: 结论

NEURAL EXCITABILITY, SPIKING AND BURSTING

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* 这篇论文发表于 1999 年，引用量已经高达两千多。Izhikevich 在该文里详细介绍了神经元兴奋性、峰值和簇发放所涉及的详细分岔机制。对于神经动力学的读者而言，该文提供了详细的理论基础。由于该文内容冗长，特意将其拆封成多个部分，以便读者准确定位到自己所需。这是 Sec. 7: 结论。

NEURAL EXCITABILITY, SPIKING AND BURSTING

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本文综述了神经元产生动作电位 (尖峰) 所涉及的分岔机制。我们展示了分岔的类型如何决定细胞的神经计算特性。例如，当稳态接近鞍-结点分岔时，细胞可以以任意低频发放全有或全无尖峰，它具有明确定义的阈值流形，并且充当积分器；即输入脉冲的频率越高，它放电的越快。相反，当稳态接近 Andronov-Hopf 分岔时，细胞在特定频率范围内发放，其尖峰不是全有或无，它没有明确定义的阈值流形，它可以响应抑制脉冲充当谐振器；即它优先响应输入的某个 (共振) 频率。增加输入频率实际上可能会延迟或终止其触发。

我们还描述了神经簇发放现象，使用几何分岔理论扩展了现有的簇发放分类，包括许多新类型。我们讨论了 burster 的类型如何定义其神经计算属性，并且我们展示了不同的 burster 可以不同地交互、同步和处理信息。

在本文中，我们回顾了参与神经元产生动作电位的相关分岔。分岔决定了神经元的可兴奋特性，从而决定了它们的神经计算特征，这些特征总结在表 1 和表 2 中。表 4 对快慢簇发放子进行了分类。其中只有少数几个，如图 126 所示，是以前被识别过，其他的是新的。

神经元：积分器或谐振器？静止状态的分岔类型决定了神经元最重要的神经计算特征：它要么是一个积分器，要么是一个谐振器。

- **积分器。**如果静止状态在不变圆分岔上通过折叠或鞍-结点消失，那么神经元就像一个积分器；输入的频率越高，它就越早放电。
- **谐振器。**如果静止状态通过 Andronov-Hopf 分岔消失，那么神经元就像一个谐振器；它更喜欢输入尖峰序列的某个 (谐振) 频率，该频率等于其特征频率的低阶倍数。增加输入的频率可能会延迟甚至终止其响应。

积分器有一个明确的阈值流形，而谐振器通常没有。积分器区分弱的兴奋性和抑制性输入，而谐振器则不区分，因为一个抑制性脉冲可以使谐振器放电。积分器可以很容易地将关于刺激强度的信息编码到它们的平均放电率中，而谐振器则不能。相比之下，谐振器对输入尖峰序列的精细时间结构很敏感，而积分器则不然，因为它们平均 (整合) 了它。奇怪的是，许多研究者试图说明生物神经元对尖峰时间的敏感性的各个方面，如巧合检测，只使用整合-放电模型。

另一个令人惊讶的事实是，积分器的许多神经计算特征，如全无放电和阈值流形，是通过研究经典的 Hodgkin-Huxley 模型引入的，它是一个谐振器，因此确实具有这些特征。

簇发放。所有簇发放的神经元似乎都有类似的行为。重复的尖峰，然后是静止的，然后是再次尖峰，以此类推。然而, 对簇发放机制的分岔分析显示，看似相似的簇发放体可以有相当不同的神经计算特性。一些簇发放体作为积分器，其他的作为谐振器。前者可能表现出簇发放同步，但可能不愿意表现出尖峰同步，而后者可以很容易地做到两者 [Izhikevich, 2000a]。因此，区分簇发放事件是很重要的。

Bifurcations	Saddle-Node on Invariant Circle	Saddle Homoclinic Orbit	Supercritical Andronov-Hopf	Fold Limit Cycle
Fold	triangular	square-wave Type I	tapered Type V	Type IV
Saddle-Node on Invariant Circle	parabolic Type II			
Supercritical Andronov-Hopf				
Subcritical Andronov-Hopf				elliptic Type III

图 126. 经典簇发放体的分岔机制。另见表 3 和表 4。

对簇发放体分类的严格尝试始于 Rinzel[1987] 的

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开创性论文，并由其他研究者扩展。这些经典簇发放体的分岔机制总结在图 126 中。由于他们的命名方案很尴尬，而且经常产生误导，我们面临着一个具有挑战性的问题，即提供一个新颖而方便的命名法。我们建议在所涉及的两个基本分岔之后命名簇发放体，见图 2。这种命名方案的优点是它对大多数科学家来说是不言自明的。

我们对簇发放体的分类对于由光滑 ODEs 描述的一维平面快慢簇发放体是完整的。由于静止状态只有六个相关的一维分岔，而平面上的尖峰状态有四个相关的一维分岔，所以只有 24 个平面快慢簇发放体，这些分岔体总结在表 3 中。它们中的每一个都可以有子类型，这取决于滞后环的类型 (图 55) 以及静止状态是在尖峰极限环吸引子的内部还是外部。

非平面簇发放体的分类可能仍然不完整。事实上，我们考虑到了所有已知的余维为 1 的相关分岔，但未来可能会发现新的分岔，这将导致新的非平面簇发放器。此外，我们没有考虑片状平滑和延迟系统中的分岔问题。最后，我们提供了一打左右这种类型的簇发放体的例子，但我们没有任何有意义的框架来进行分类。

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